

SOCIAL MODIFICATIONS RELATED TO RARENESS IN ANT SPECIES¹

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In the evolution of true sociality in insects, one potentially disadvantageous side effect is the reduction of the effective population size. As a result of sociality, the reproductive individuals are longer lived and the populations more stable, but these features have been achieved by converting most of the adult population into the sterile supporting worker caste. In the case of the social Hymenoptera, the effective size of a discrete population is clearly not the same as the number of adult individuals. It must be derived in relation to the existing nest queens and the males (mostly no longer living) that contributed, during the nuptial flights, to the sperm now living in the spermathecae of the queens. In population genetics the *effective population size*, \bar{N} , is defined (cf. Li, 1955, p. 320) as the equivalent "ideal" population containing N breeding individuals, half of them females and half males, mating at random. The variance of the random deviation of gene frequencies is therefore $p(1-p)/2N$; and the rate of loss of heterozygosis $1/2N$. When the N breeding individuals are not evenly divided between the sexes, \bar{N} is less than N . Where N_0 and N_1 are the numbers of female and male parents respectively,

$$\bar{N} = \frac{4N_0N_1}{N_0 + N_1}.$$

Let us refer to the number of nest queens in a population of an ant species as Q and the number of males that participated in their fertilization as M ; the average number of queens contributing to single colonies will be \bar{Q} ; \bar{M} will be the average number of males fertilizing each queen; and $\bar{M}\bar{Q}$

will then be the average number of males contributing to a single colony, on the reasonable assumption (for ants) that normally each male fertilizes no more than one queen. Let N_t be the total number of adult individuals, of all castes, in the population, and N_c the average number of adult individuals per colony. Then N_t/N_c is the number of colonies in the population, while

$$Q = \bar{Q} \frac{N_t}{N_c}; \text{ and } M = \bar{M} \bar{Q} \frac{N_t}{N_c}.$$

The effective size of the population can be derived from the general equation just given as

$$\bar{N} = \frac{4N_t}{N_c} \left(\frac{\bar{M}\bar{Q}}{1 + \bar{M}} \right).$$

As \bar{M} , the average number of males fecundating each queen, becomes very large, \bar{N} approaches the limit, $4\bar{Q}N_t/N_c$. Thus, \bar{N} increases as a simple multiple of the average number of nest queens. An increase in \bar{M} , on the other hand, provides a significant gain only in the first steps. For example, increasing \bar{M} from one to two increases \bar{N} by 33%, but increasing \bar{M} from nine to ten increases \bar{N} by only 1%. At the most, \bar{N} can be doubled by increasing \bar{M} , and half of this gain is already achieved by changing \bar{M} from one to three.

The effective population size of some ant species is very low. In the Oropouche Cave population of *Erebomyrma urichi*, it is estimated not to exceed 400 (Wilson, 1962). The population of *Lasius minutus* at Hidden Lake, Michigan, nests in only 700 mounds (Kannowski, 1959a). Since a single colony occupies an average of about 4.4 mounds (Kannowski, 1959b) and each colony probably contains a single queen, the population can be estimated to contain approximately 160 colonies and an effective

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tive population size of as low as 320 outside the reproductive season. The extreme rarity of many social parasites, coupled with patchy distributions, has long been noted by myrmecologists. A typical example is *Manica parasitica*, recorded only from nests of *M. bradleyi* on the top of Polly Dome, Yosemite National Park, California, and apparently absent from immediately surrounding areas (Creighton, 1934; Wilson, pers. obs.). Chamberlin (in Wheeler, 1910) found *Symmyrmica chamberlini* only "in several parts of a ten-acre field" near Salt Lake City, Utah, in 1902, and only three colonies were discovered there; the species has not been collected since. The extreme parasite *Teleutomyrmex schneideri* has one population apparently limited to the east side of the isolated Saas-Fee Valley of Switzerland, between 1,800 and 2,300 meters altitude (Kutter, 1950); a second population has been discovered near Briançon in the French Alps (Collingwood, 1956).

These rare species are of interest with reference to the question of whether they have undergone social modifications that increase effective population size. With a fixed low N_t , the species face two related problems specifically aggravated by the social condition: (1) the danger of irreversible reduction of population size outside the reproductive season, which is most of the year, and (2) the danger of irreversible reduction of genetic variability due to inbreeding and hence contributing to (1). We might inquire first whether social structure has been modified to increase \bar{N} within the limits of a fixed N_t , and then whether special devices have been evolved to increase exogamy. These two adaptive "goals" are not incompatible. Theoretically, they can be reached by interdemic selection, although such a process would be most difficult to demonstrate in nature (see Wright, 1960). From the equation just given, it can be seen that \bar{N} can be increased by decreasing the average colony size (N_c), by increasing polyandry (i.e., increasing \bar{M}), and by increasing the number of functional queens in each colony ($\bar{Q} > 1 = \text{polygyny}$). Ex-

ogamy, which also increases \bar{N} , can be promoted by various behavioral modifications such as large mixed swarms (e.g., as illustrated in the observations of Kanno-ski, 1958 and Marikovsky, 1961); by dioeciousness, or the production of only one reproductive sex by a colony in a given year (Marcus, 1949; Scherba, 1961; Marikovsky, 1961); by protandry, or the earlier production and release of males from a given colony (Talbot, 1956, 1959); and by a tighter synchronization of the nuptial flight among colonies. Note that the quantitative effects of the various modifications differ. By changing \bar{M} from one to a very large number, \bar{N} is doubled. The same relatively slight effect is achieved by passing from complete inbreeding to wholly random mating through exogamy. Much larger, but not unlimited, gains are possible through polygyny and reduced colony size.

Have in fact the rare ant species taken these steps? To test the hypothesis, three categories of rare species have been recognized (bog endemics, cave ants, permanent social parasites), and biological characteristics of the adequately known representatives noted from the literature. (Of the bog species, only *Lasius speculiventris* is truly rare over its whole range. The remaining three species are local, i.e., divided into small, "bog-endemic" demes only in the part of the range where they were studied.) Each species was compared with the commoner representatives of its genus or with the nearest taxa that showed differences. The results are summarized in table 1. On the basis of the available sample, it would appear that colony size is not ordinarily modified, nor is there any detectable trend toward dioeciousness, protandry, or closer synchronization of nuptial flight. Descriptions of mating behavior are not numerous enough to draw any conclusion about polyandry. There is a strong trend toward polygyny, as predicted. With the clarity of hindsight, this would indeed seem intuitively to be the "easiest" way to increase \bar{N} , since it is the most effective of the possible modifications and requires no

TABLE 1. The characterization of rare ant species with respect to certain social features that affect reproductive population size

- (+) the species shows a significant difference in the direction indicated at the head of the column from commoner members of the genus or from the nearest related taxa.
 (−) the reverse is true, i.e., the species shows the opposite departure from related taxa.
 (0) no difference.
 (---) information is available but the comparison is meaningless because worker caste is lacking.
 (?) sufficient information not available.

Species	Reference	Predicted devices to increase N			Predicted devices to increase exogamy		
		Decreased colony size	Polygyny	Polyandry	Special behavioral devices to increase exogamy	Dioeciousness, or protandry	Increased synchronization of mating activity among colonies
Bog "endemics"	Kannowski						
<i>Leptothorax muscorum</i>	(1959a)	0	+	?	?	?	?
<i>Lasius minutus</i>	"	0	0?	?	?	?	0
<i>L. speculiventris</i>	"	0	0?	?	~	?	0
<i>Formica neorufibarbis</i>	"	0	+	?	?	?	0?
Cave species (troglophilic)							
<i>Erebomyrma urichi</i>	Wilson (1962)	0	+	?	?	?	?
Parasitic species	Wilson and						
<i>Kyidris yaleogyna</i>	Brown (1956)	0	+	?	?	0	?
<i>Formicoxenus nitidulus</i>	Wheeler (1910); Stumper (1921)	0	+	?	~	0	?
<i>Wheeleriella santschii</i>	Forel (1906)	---	0	?	~	0	?
<i>Anergates atratulus</i>	Wheeler (1910); Gösswald (1932)	---	+	?	~	0	0
<i>Teleutomyrmex schneideri</i>	Kutter (1950); Stumper (1950)	---	+	+	~	0	0
<i>Epimyrmica stumperi</i>	Kutter (1951); Stumper and Kutter (1951)	---	+	?	?	?	?
<i>Plagiolipsis xene</i> and <i>P. grassei</i>	Kutter (1952) LeMasne (1956)	---	+	?	~	0	0
<i>Bruchomyrma acutidens</i>	Bruch (1931)	---	+	?	~	0	0

radical reorganization of the colonial economy as decreased colony size might. As an illustration, adding two extra queens has a greater effect than reducing the colony size by one-fourth. The trend to polygyny is even stronger than a first inspection would suggest. The monogynous species (*Wheeleriella santschii*, possibly also *Lasius minutus* and *L. speculiventris*), are also temporary social parasites, which show marked hostility toward host queens during colony founding. Hence, in these species monogyny has a special advantage. The fourth temporary social parasite in the

list of rare species, *Epimyrmica stumperi*, is polygynous only by virtue of adding fertile queen-worker intercastes after colony foundation.

But contrary to the prediction, rare ant species have reduced exogamy. Mating among members of the same colony, which in effect makes the colony somewhat like a self-fertilizing hermaphrodite, has long been recognized by myrmecologists as a trait of rare parasitic species. The males are commonly apterous or subapterous, mating takes place in or near the nest, and the fecundated winged queens then dis-

perse in search of new host colonies or else return to the old. Whether intracolony mating characterizes other categories of rare species is an open question. Since the trait must cause a decrease in \bar{N} , just the reverse of what purely logical considerations concerning population size alone dictate, it is necessary to consider other possible advantages of such a design feature. At least one can be deduced: intracolony mating certainly eliminates the loss of virgin reproductives that normally occurs during dispersal and thus insures that queens will be fecundated, however scarce the species. This advantage can easily outweigh the disadvantage from inbreeding. As just noted, passing from random mating to perfect inbreeding only reduces \bar{N} by half, a deficit that could be balanced by doubling the average number of nest queens. The extent of true brother-sister mating (adelphogamy) is unknown. Because of the additional trait of polygyny in these same species, the offspring of several matings probably breed with each other as a matter of course. In fact, parasitic species may be less "adelphogamous" than previously assumed, since in most cases it has not been established with certainty that true brothers and sisters within polygynous colonies really mate with each other at all. In polygynous colonies the opposite case is conceivable. It is further conceivable that for the same adaptive reasons polyandry is also increased in the species that mate intracolony.

These relationships are of interest because they show the possibility of modifications of social behavior as a consequence of reduced population size. However, while the relationships are established to a limited degree, the suggested causation is not proven. Other causations, as for instance peculiarities in the phenomenon of parasitism promoting adelphogamy, may exist but have not been suggested. It has been my purpose here to collate scattered information with reference to one exactly stated evolutionary hypothesis, and thereby to point out certain gaps in our informa-

tion that may prove of future significance in the pursuit of this interesting subject.

SUMMARY

The risk associated with small deme size in rare species is increased in social insects, in which large proportions of the populations are converted into the sterile worker caste. Several modifications in social organization can be deduced which would increase the effective population size and, in a system otherwise unaltered, decrease the risk. Available information on rare ant species, especially the relatively well-known social parasites, has been systematically examined to test these predictions. Polygyny, the occurrence of multiple queens in single colonies, and seemingly the most effective of the possible devices, is more frequent in nature, as predicted. Colony size does not appear to be modified. Contrary to the prediction, behavior is modified to increase endogamy (colony inbreeding) rather than to decrease it. It is suggested that this serves the function of reducing another, greater risk associated with rareness; namely, that the sexual forms will not meet at all. Available data on other aspects of sexual behavior that relate to the subject are as yet inadequate. Finally, it is only a hypothesis, subject to further verification, that the relations established are causal ones.

LITERATURE CITED

- BRUCH, C. 1931. Notas biológicas y sistematicas acerca de "*Bruchomyrma acutidens*" Santschi. Rev. Mus. La Plata, **33**: 31-55.
- COLLINGWOOD, C. A. 1956. A rare parasitic ant (Hym., Formicidae) in France. Ent. Month. Mag., **92**: 197.
- CREIGHTON, W. S. 1934. Descriptions of three new North American ants with certain ecological observations on previously described forms. Psyche, **41**: 185-200.
- FOREL, A. 1906. Moeurs des fourmis parasites des genres *Wheeleria* et *Bothriomyrmex*. Rev. Suisse Zool., **14**: 51-69.
- GÖSSWALD, K. 1930. Die Biologie einer neuen Epimyrmaart aus dem mittleren Maingebiet. Z. wiss. Zool., (A) **136**: 464-484.
- . 1932. Ökologische Studien über die Ameisenfauna des mittleren Maingebietes. Z. wiss. Zool., (A) **142**: 1-156.

- KANNOWSKI, P. B. 1958. Swarming of the ant *Stenamma brevicorne* (Mayr). Ent. News, **69**: 231-233.
- . 1959a. The flight activities and colony-founding behavior of bog ants in southeastern Michigan. Insectes Sociaux, **6**: 115-162.
- . 1959b. The use of radioactive phosphorus in the study of colony distribution of the ant *Lasius minutus*. Ecology, **40**: 162-165.
- KUTTER, H. 1950. Über eine neue, extrem parasitische Ameise 1. Mitteilung. Mitt. Schweiz. Ent. Ges., **23**: 81-94.
- . 1951. *Epimyrma stumperi* Kutter (Hym. Formicid.) 2. Mitteilung. Mitt. Schweiz. Ent. Ges., **24**: 153-174.
- . 1952. Über *Plagiolexis xene* Stärcke (Hym. Formicid.). Mitt. Schweiz. Ent. Ges., **25**: 57-72.
- LEMASNE, G. 1956. Recherches sur le fourmis parasite: le parasitisme social double. C.R.S. Acad. Sci. (Paris), **243**: 1243-1246.
- LI, C. C. 1955. Population genetics. Univ. Chicago Press.
- MARCUS, H. 1949. Como las hormigas evitan el incesto. Folia Univ. Cochabamba (Bolivia), **3**: 95-96.
- MARIKOVSKY, P. I. 1961. Material on sexual biology of the ant *Formica rufa* L. Insectes Sociaux, **8**: 23-30.
- SCHERBA, G. 1961. Nest structure and reproduction in the mound-building ant *Formica opaciventris* Emery in Wyoming. J. New York Ent. Soc., **59**: 71-87.
- STUMPER, R. 1921. Recherches sur l'ethologie du *Formicoxenus nitidulus* Nyl. Bull. Soc. Ent. Belg., **3**: 90-97.
- . 1950. Les associations complexes des fourmis. Commensalisme, symbiose et parasitisme. Bull. Biol. Fr. Belg., **84**: 376-399.
- AND H. KUTTER. 1951. Sur l'ethologie du nouveau myrmecobionte *Epimyrma stumperi* (nov. spec. Kutter). C.R. Acad. Sci. (Paris), **233**: 983-985.
- TALBOT, M. 1956. Flight activities of the ant *Dolichoderus (Hypoclinea) mariae* Forel. Psyche, **63**: 134-139.
- . 1959. Flight activities of two species of ants of the genus *Formica*. Amer. Midl. Nat., **61**: 124-132.
- WHEELER, W. M. 1910. Ants. Columbia Univ. Press.
- WILSON, E. O. 1962. The Trinidad cave-ant *Erebomyrma* (= *Spelaemyrmex*) *urichi* (Wheeler), with a comment on cavernicolous ants in general. Psyche, **69**: 62-72.
- AND W. L. BROWN. 1956. New parasitic species of the ant genus *Kyidris* from New Guinea. Insectes Sociaux, **3**: 439-454.
- WRIGHT, S. 1960. Physiological genetics, ecology of populations, and natural selection. In S. Tax ed., Evolution after Darwin, vol. 1, p. 429-475.